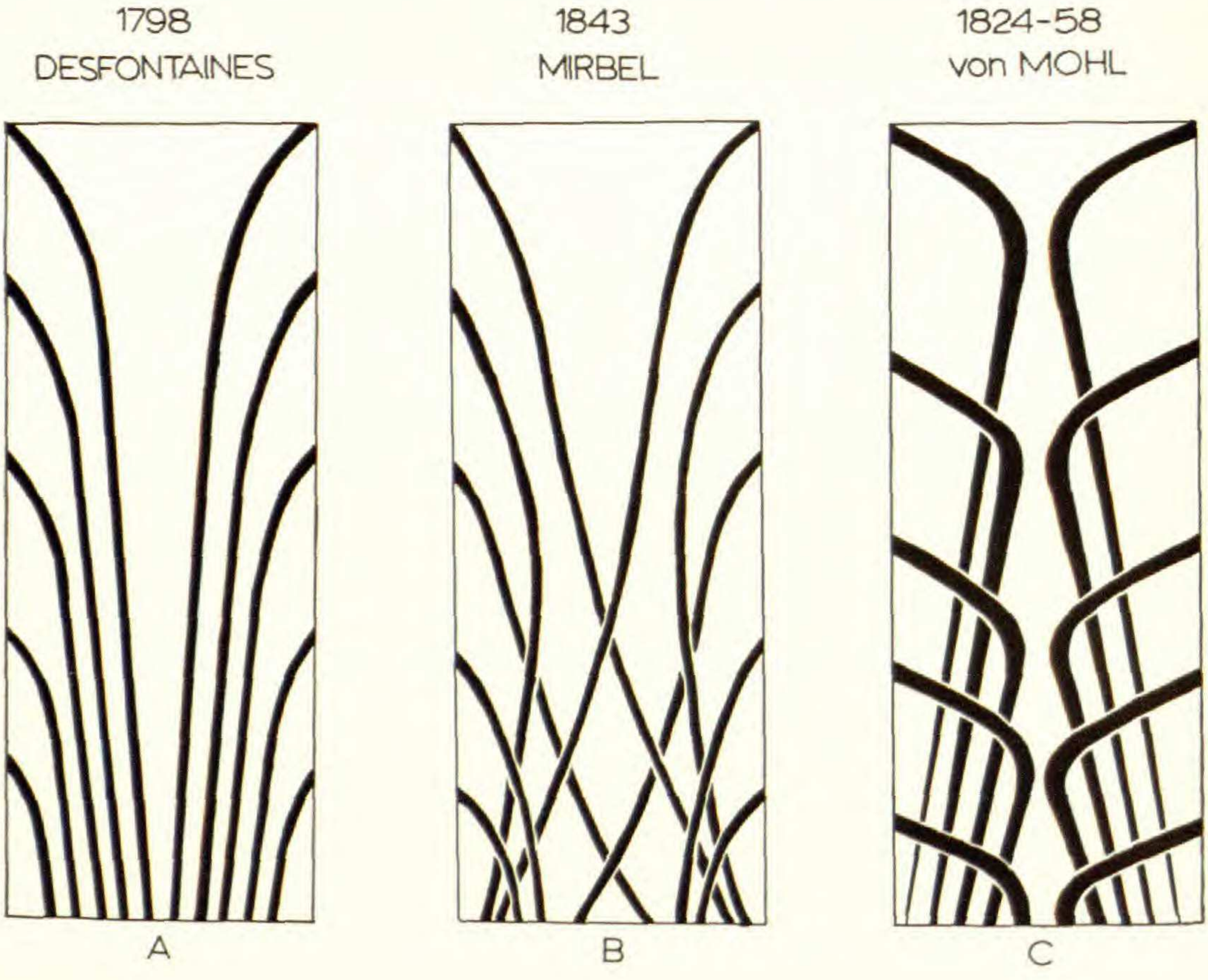
1798
DESFONTAINES
1843
MIRBEL
1824-58
von MOHL
A
B
C
1876
FALKENBERG
1877
de BARY
1884
HABERLANDT
X
D
E
F

south Florida. Aërial stems 2–3 cm. in diameter and up to 5 m. high arise from horizontal rhizome segments up to 1 m. long. Younger, developing parts of each rhizome segment are protected by short, rigid scale leaves which are morphologically equivalent to the sheathing base of the foliage leaves of aërial stems. In older parts of rhizomes the scales decay, leaving annular scars at intervals of 1–3 cm. marking the nodes. Adventitious roots arise at wide but fairly regular intervals along the rhizome, commonly, but not exclusively at the nodes. After a period of horizontal growth the apical part of the rhizome enlarges appreciably and turns erect. There is a rapid change from rhizome scales to normal foliage leaves, the transitional leaves with increasingly developed blades illustrating that the scales are essentially foliage leaf sheaths without a blade. In the axils of several of the most distal rhizome scales new vegetative buds grow out as the rhizome apex turns upwards. Most of these lateral branches grow out horizontally as new rhizome segments; occasionally they grow erect as additional aërial stems. In the aërial shoot early growth is wholly vegetative, the foliage leaves subtending either no buds or, at the most, aborted inflorescences. The subsequent detailed account of the distribution of the vascular bundles deals entirely with this part of the stem uncomplicated by fully developed inflorescence insertions. In the distal parts, axillary inflorescences appear, internodes are shortened

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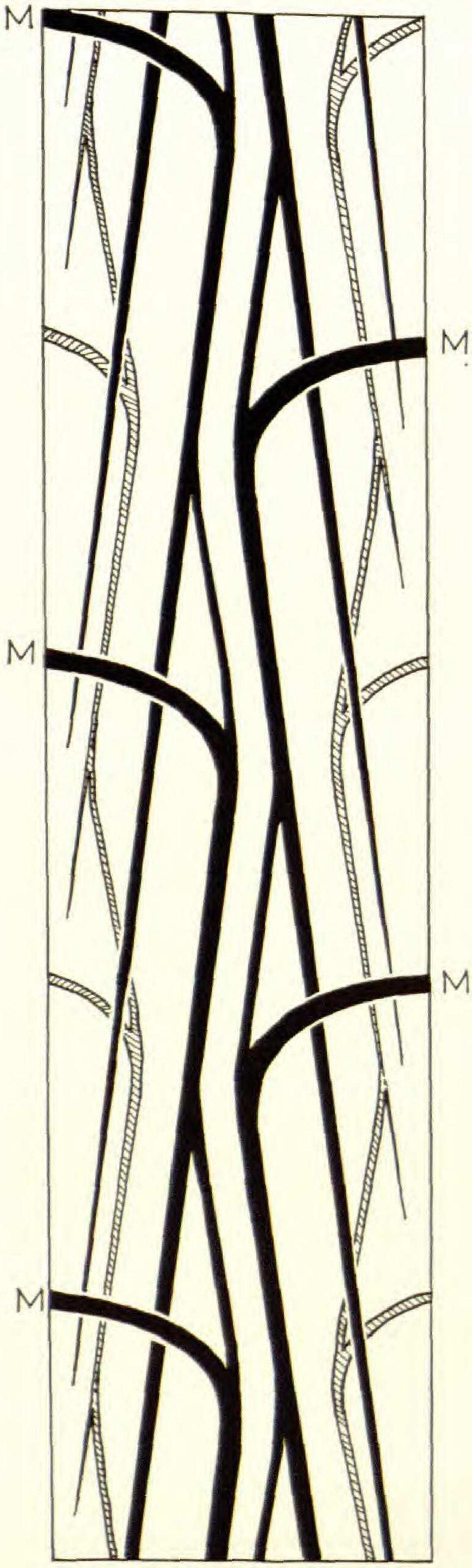
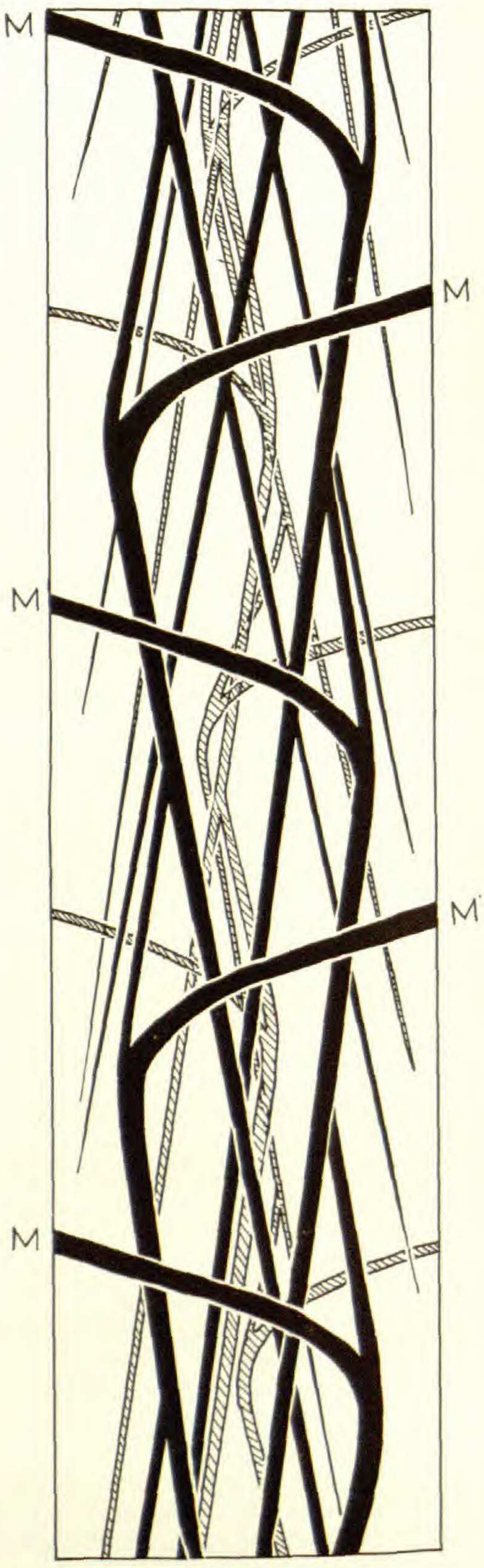
FIG. 1. Hypothetical bundle course of "palm type" according to various classical authors. A–E, redrawn from Monoyer, 1925; F, from Haberlandt, 1884. A. *Desfontaines* (1798). All bundles proceed to base of stem with a distal curve becoming parallel to the vertical axis of the stem below. Developmentally new bundles were supposed to arise in the stem center and crowd older bundles towards the periphery. B. *Mirbel* (1843). Two categories of bundle, the first extending from one side of stem to the opposite, the second restricted to one side of stem (see text p. 171). All bundles proceed to the base of the stem. C. *Von Mohl* (1824). All bundles proceeding to the base of the stem, all alike, initially curving abruptly towards the center and subsequently passing very gradually back to the periphery and ending blindly below. Later (1849) he suggested that the lower extremities of bundles might fuse. With either scheme the number of bundles at any one level remains relatively constant. D. *Falkenberg* (1876). Purporting to illustrate *Chamaedorea elatior* (and possibly derived from Nägeli, 1858, who studied this species), although, according to his text, Falkenberg studied only *Chamaedorea schiedeana*. Several categories of bundles, all ending blindly below, some extending much deeper into the stem than others. Dotted line represents boundary between cortex and central cylinder. E. *De Bary* (1877). A scheme derived directly from Von Mohl, without reference to Falkenberg's article. Considered according to a distichous phyllotaxis; dorsal bundles penetrating deeply, ventral bundles penetrating less deeply into the stem center. At "X" a tentative fusion is illustrated without comment. Diagrams in a number of modern textbooks appear to be based upon this diagram and incorporate a regular system of bundle fusions which have been inferred but never observed. F. *Haberlandt* (1884). From Falkenberg (1876), via Sachs (1882). A much-reproduced illustration purporting to represent the "palm type." It was actually drawn by Falkenberg to represent *Aspidistra elatior* (Liliaceae), a statement omitted from textbooks. It seems to bear little relation to actual palms. From this date on, the "palm type" of vascular construction has become entirely hypothetical.

MONOYER 1925



BASE



APEX

and the outline of the stem becomes more angular owing to the pressure of developing inflorescences. The anatomy of this part of the stem will be described in a subsequent article.

By choosing a palm of this stature the problem was reduced from the analysis of a stem like that of *Cocos*, which may be up to 0.5 m. in diameter with over 20,000 vascular bundles at any level, to one in which there were about 1,000. The relative ease with which the *Rhapis* stem could be sectioned freehand was a second reason for its selection. Clearly, principles based on the study of a diminutive palm must be verified by analysis of a much larger and more typical stem. The basic approach used in this work suggests that ultimately this will be possible. However, we already have much evidence from larger palms like *Chrysalidocarpus*, *Sabal*, *Washingtonia*, etc. which suggests that *Rhapis* is indeed a small-scale model for palm stems generally.

CINEMATOGRAPHIC ANALYSIS

Cinematographic analysis was accomplished by two different methods, namely, by photographing, frame by frame, (1) sequentially cut surfaces and (2) serial sections through the microscope. Kodachrome II, Type A film has been used throughout.

Surface photography. Photography of cut surfaces has been used only to a very limited extent with *Rhapis*. Pieces of stem were clamped in the specimen holder of a Reichert type OME sliding microtome, and thin shavings were taken with a frequently sharpened knife. The specimen holder was advanced for each cut along the optical axis of the camera, i.e., manually with the screw which raises the specimen holder. The specimen holder was modified in order to accept long pieces of stem. A scale marked in ink on the stem provided a means of measuring the rate of advance. The camera, a Bolex H 16 REX, was mounted on a sturdy stand above the specimen with the optical axis coinciding with that of the stem. A long focal-length lens (105 mm.) allowed the operator of the microtome ample working space. We developed this method ourselves but learned during the preparation of this manuscript that a similar, but automatic method for the analysis of short tissue pieces had been developed earlier by Postlethwait. In fact, the method seems to have been proposed as long ago as 1907 (Postlethwait, 1962).

Photography of serial sections. For the analysis of the course of

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FIG. 2. Course of vascular bundles in *Arecastrum romanzoffianum* (*Cocos botryophora*), according to Monoyer, 1925. Redrawn and slightly modified. *Base*. May be compared with De Bary's scheme, but with the addition of fusion bundles (*faisceaux de jonction*) which unite upper and lower bundles. M's (solid black) represent dorsal (major) bundles which penetrate most deeply into stem center. Ventral and minor bundles (cross hatched) have same course but penetrate less deeply into stem. Bundles are shown as ending blindly below. *Apex*. Essentially as in base but with bundles of both systems all extending more than halfway across stem. A likely explanation of this is given in the text (p. 171).

vascular bundles over long distances, sections 25–50μ thick were cut freehand on the same microtome at intervals of 0.5 mm. The automatic feed was set at 50μ and every 10th section kept. For easy processing each of the sections retained was tied with a constant orientation to a sequentially numbered slide by cotton thread. Orientation was facilitated by a shallow longitudinal groove scored along the stem and visible as a slight notch in each section. A small wad of glass wool between cotton thread and section prevented unstained thread marks across the section. Sections were bleached briefly in "Clorox," washed in water and 70% ethanol, stained overnight in a mixture of safranin (95 parts of a 1% solution in 70% ethanol) and Delafield's haematoxylin (5 parts), differentiated briefly in acidulated 50% ethanol, dehydrated, and mounted in neutral "Piccolyte." Sections at 0.5 mm. intervals proved adequate for general analyses as it was easy to trace a single bundle from section to section. For details of "rapid" changes which occurred at a node a complete series of sections approximately 30μ thick were prepared, passing through an entire internode about 2 cm. long which had been embedded in celloidin.

A piece of stem much longer than could be held complete in the microtome clamp was analyzed in shorter lengths. The upper part of each of these shorter segments was clamped in the normal way and as many sections as possible removed, then the lower part was held firm by freezing, in a 5% gum arabic solution, to the flat stage of a freezing attachment and the sectioning of the segment completed. We have now greatly simplified the procedure by the development of a modified clamp with which very long pieces of stem can be held.

The key problem is to match successive sections under the microscope so that a fixed point in the section successively occupies the same position on each frame of the film. So far this has been done by incorporating a camera lucida into the microscope-camera system in such a way that an outline drawing of every 2nd to 6th section is made and used to orient its successors precisely. The drawings are used as an additional permanent record, with the microscope-stage coordinates marked for about every 10th slide, so that, if necessary, it is possible to return to the slides at any later time and locate the photographed position. A Wild M20 microscope was used, with the parts assembled from below upwards as follows: microscope base with centerable rotating mechanical stage, objective turret, drawing tube, camera tube H, binocular. Viewing and focusing are done in the binocular; photographs are taken with a Bolex H 16 REX, which is mounted on a Wild camera stand.

It is often not necessary to have a permanent record of drawings and photographed slide positions. The extra labor of drawing can be eliminated with an optical "shuttle" system. A Wild discussion tube is mounted upside down on two microscopes; the images from these two microscopes are thus brought into a single camera and viewing system. Photographs are taken alternately through each microscope, the double image being used merely to superimpose successive sections precisely.

Analysis of films. For the analysis of films an L-W 224 A Photo-Optical Data Analyzer was used. This is essentially a 16 mm. movie projector modified by L-W Photo, Inc. (15451 Cabrito Road, Van Nuys, Calif.), so that a film can be projected without flicker at any speed from 1 to 24 frames per second, forward or backward. The film can be stopped instantly, and moved frame by frame. Less expensive projectors are available, and action editors are also usable for the purpose. However, the instrument we have used has proved ideal in every respect.

The vascular system of *Rhapis* described below has been resolved by an essentially dynamic process. This is reflected in the subsequent description which refers to the distribution of vascular bundles by a dynamic terminology. This is merely a convention. Changes in direction of mature bundles reflect changes in the angle of differentiation of bundles in meristematic regions. "The "movement" suggested by ciné analysis, particularly of one bundle in relation to another, is quite apparent and implies neither actual movement of bundles nor their growth.

GENERAL STEM ANATOMY OF RHAPIS

Stem (FIG. 7) divided into a narrow cortex less than 1 mm. wide and a broad central cylinder (15–30 mm. wide). Epidermis uniform, cells cubical or slightly tabular and somewhat elongated vertically; slightly anticlinally extended; outer wall thickened, wholly cutinized. Epidermal cells occasionally with lignified walls. Hypodermis of 2–4 layers of narrow cells scarcely differentiated from rest of cortical parenchyma but becoming thick-walled, lignified and conspicuously pitted in old stems and forming a continuous thin mechanical layer except for interruptions below occasional stomata. Cortical parenchyma up to 20 cells deep; cells isodiametric or slightly elongated vertically, becoming chlorenchymatous in exposed stems. Innermost layers of cortical parenchyma sometimes slightly lignified. Fibers common as thick-walled strands scattered throughout cortex. Peripheral strands narrow, purely fibrous, wider strands toward central cylinder often including a narrow phloem strand, or both xylem and phloem, and so transitional to cortical vascular bundles. Most leaf traces passing across cortex and entering central cylinder.

Central cylinder not delimited sharply from cortex by endodermis, parenchyma sheath or other specialized layer but by peripheral densely congested vascular bundles forming peripheral mechanical zone. Each peripheral bundle with a massive fibrous sheath; xylem sheathed only by narrow slightly thick-walled parenchyma cells. Bundles irregularly rhombohedral in transverse section, separated by narrow bands of short, slightly thick-walled pitted and subsequently lignified ground parenchyma cells, forming a reticulum between the congested bundles continuous externally with cortical parenchyma and gradually transitional internally to thin-walled somewhat looser, unlignified ground parenchyma of isodiametric or slightly elongated cells. Peripheral mechanical zone traversed by conspicuous leaf traces and associated bundles (vertical, bridge, and satellite bundles — see below). Vascular bundles towards center of stem gradually less congested and with reduced fibrous sheaths, becoming more circular in transverse outline. Isolated narrow fibrous strands very rare. Silica bodies in small isodiametric stegmata abundant next to fibers.

Tannin common in unmodified parenchyma cells throughout the stem; rhaphide-sacs occasional. Starch often abundant in ground parenchyma.

Vascular bundle (the following refers to a central bundle, variation in its anatomy throughout its length is discussed in detail below): abruptly delimited from ground parenchyma by sheathing tissues. Phloem usually directed towards stem periphery, partly sheathed by fibers forming a well-developed fibrous phloem sheath. Fibers becoming sclerotic and conspicuously concentric-layered with age; lignification and wall thickening appearing first in innermost fibers closest to phloem and subsequently in centrifugal fibers. Conducting phloem tissue, often divided into two equal strands by a narrow sclerotic isthmus, including sieve tubes mostly 12–15μ wide, with compound sieve plates on slightly oblique to oblique end walls, irregularly scattered companion and phloem parenchyma cells, the former not well differentiated from the latter. Protophloem remains often recognized as an irregular group of sclerotic cells in the peripheral part of the sclerotic isthmus. Xylem enclosed by thin-walled, slightly lignified parenchyma less abruptly delimited from ground tissue than phloem sheath; rarely including a few fibers. Cells immediately surrounding vessels with wide pits and distinctly differentiated from remaining xylem parenchyma. Tracheal elements[3] including one or two metaxylem vessels 40–60μ wide, circular in transverse outline, and usually some narrow protoxylem elements. Protoxylem often separated from metaxylem by a narrow parenchymatous isthmus. Metaxylem vessel elements 600–800μ long with mostly scalariform perforation plates with few (4–10) thickening bars on oblique end walls; protoxylem either long imperforate tracheids with annular or helical wall thickenings or somewhat shorter vessels with unspecialized perforation plates transitional to metaxylem elements.

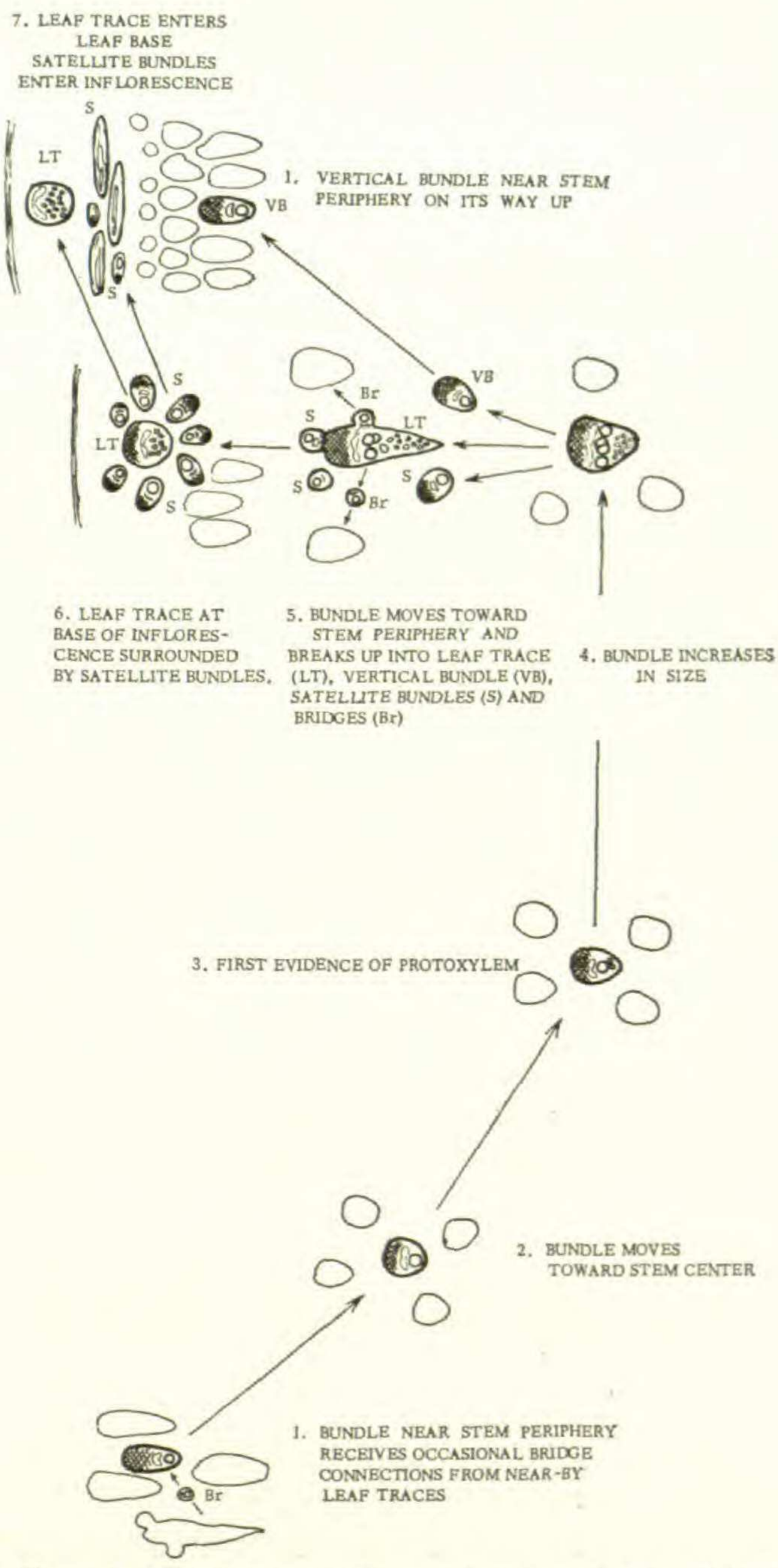
Variation throughout a single stem largely involves an increase in lignification with age. Stems vary much in vigor of growth and this is reflected in differences in diameter and length of internodes and total number of vascular bundles. Absolute measurements may be misleading, the best comparative unit is the internode. Differences between axes in juvenile and adult stages of growth have not yet been examined. The following paragraphs deal with overall distribution and types of vascular bundles in the adult mature stem; subsequently anatomical changes along vascular bundles are described.

COURSE OF VASCULAR BUNDLES IN THE STEM

Cinematographic analysis demonstrates that *all vascular bundles behave essentially alike* (FIG. 3). Major and minor bundles, with a continuous transitional series, differ in relative position in the stem and in the number of internodes between their successive branchings. Any one leaf is supplied by a larger number of minor and a smaller number of major bundles.

From the base to the apex essentially *all bundles maintain their individuality and proceed indefinitely up the stem.* Each of these *vertical*

[3] Protoxylem is distinguished from metaxylem entirely by its position and the nature of its elements. Developmental differences are not considered here.



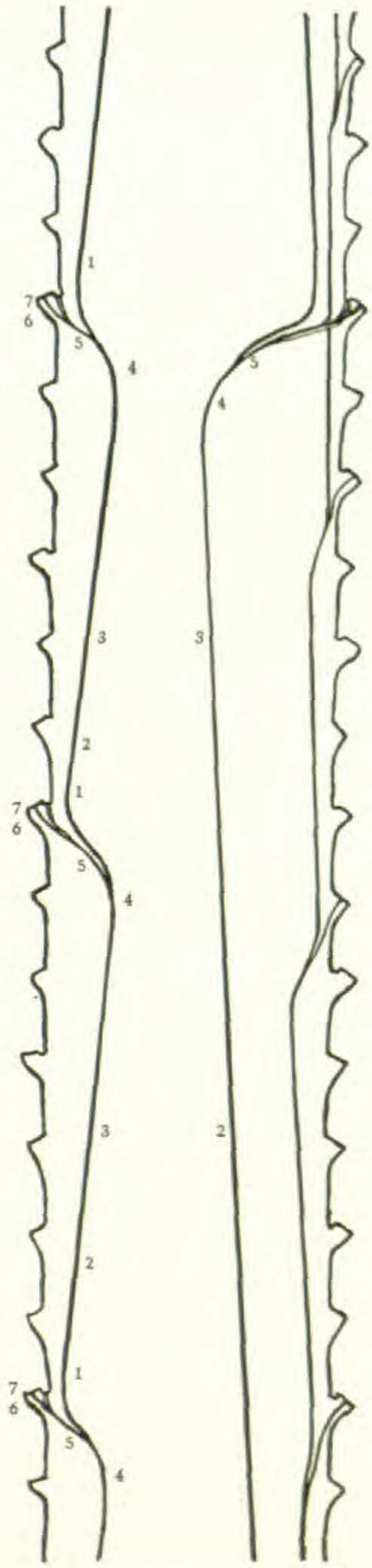
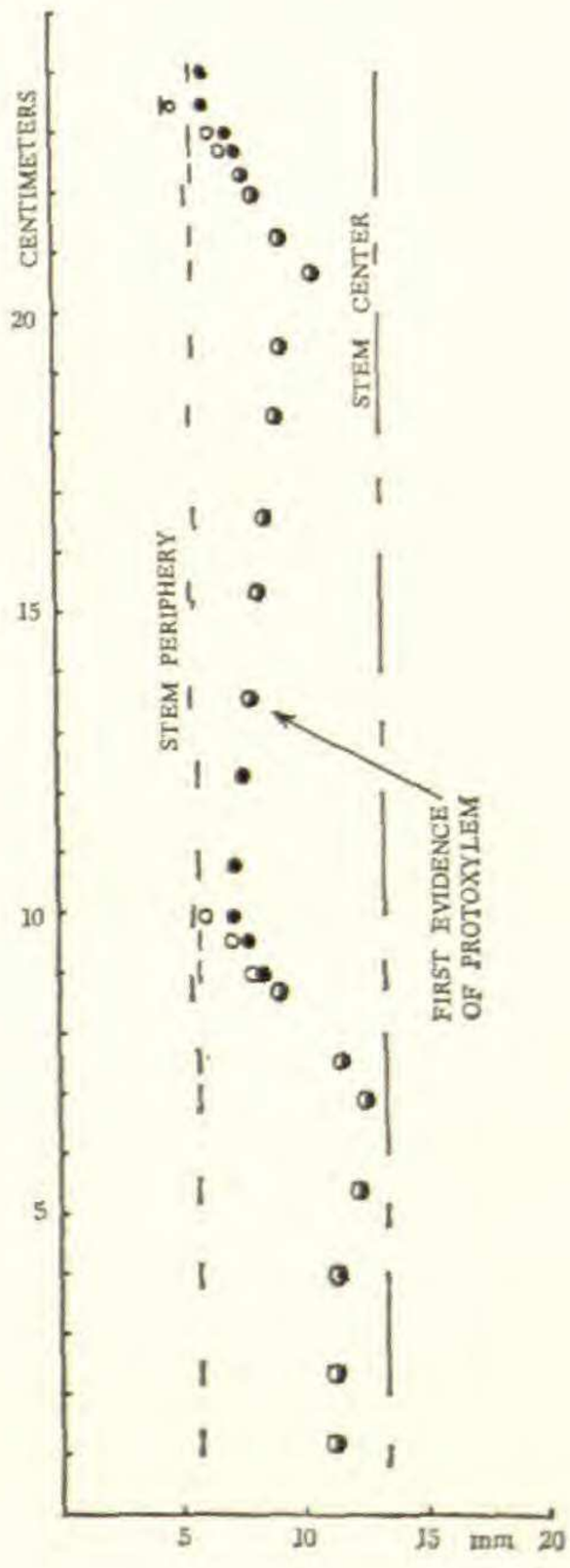


FIG. 3. The course of vascular bundles in the stem of *Rhapis excelsa*. In the diagram on the right the stem axis is foreshortened four times in relation to the stem diameter.

bundles gives off a *leaf trace* at intervals, the minor giving off leaf traces more frequently than the major bundles (FIG. 3, right). The overall course of the bundle is not a straight line. Each vertical bundle "moves" slowly towards the stem center. At intervals which vary according to its status, the bundle is "pulled out" sharply towards the periphery. Major bundles extend well into the stem center, minor bundles are "pulled out" before they reach very far toward the stem center (FIG. 3, right). The fact that only relatively few bundles reach the stem center, but all

bundles are at one time or another in the peripheral region, results in a considerable crowding of the peripheral stem area. This crowding is accentuated by the large fibrous sheaths of the bundles in this area (FIG. 7).

FIGURE 4 represents to scale, a bundle with a distance of 135 mm. between successive *leaf contacts*. Distances between leaf contacts are shorter in minor bundles, longer in major bundles. A major bundle was traced incompletely, but by extrapolation it was estimated that the distance between two successive leaf contacts was approximately 45 cm. The interval between successive leaf contacts is by no means uniform along a given bundle. Major bundles can become minor bundles and vice versa.



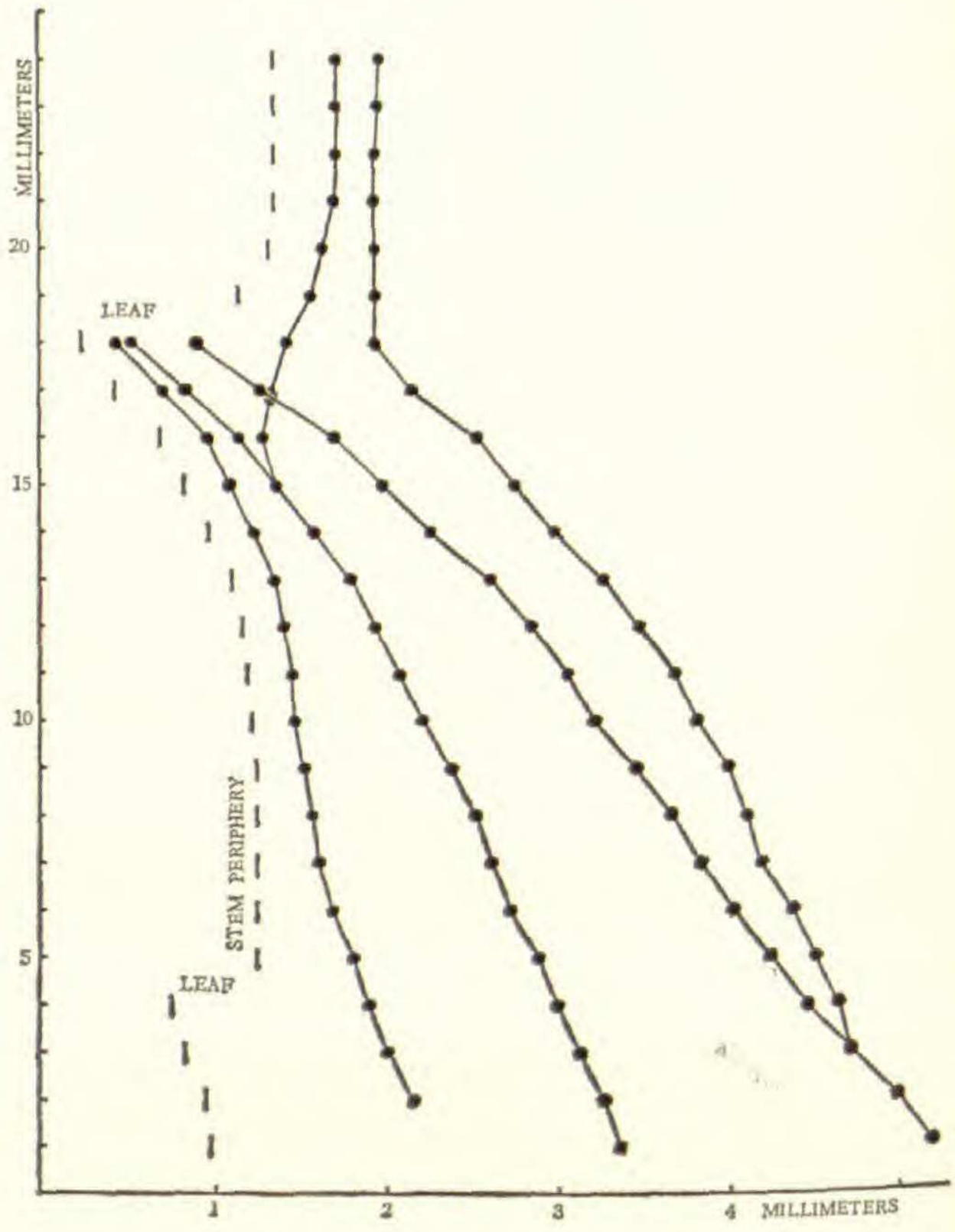


FIG. 4 (left). The course of a vascular bundle in the stem of *Rhapis*, drawn to scale. For convenience the stem axis is foreshortened four times in relation to the stem radius. Measurements were taken on the microtome sections after positions of the bundle had been secured with the aid of the analytical film and the drawings. Because there is no fixed reference point in the palm stem, outermost vertical bundles were taken as straight, and distances taken to the stem periphery (short vertical lines) and the measured bundle. Open circles indicate presence of protoxylem only; half-open circles indicate presence of both protoxylem and metaxylem; closed circles indicate presence of metaxylem only.

FIG. 5 (right). Diagram of a major, an intermediate, and a minor leaf trace to show spatial relationship to each other. Bridges and satellite bundles are not shown. Stem axis is foreshortened 3.6 times in relation to the stem radius. Measurements were taken as in FIG. 4.

A feature which cannot be indicated in FIGURE 3 is the shallow helix exhibited by all bundles in the central, uncrowded part of the stem. Traced upwards, all central bundles rotate uniformly in a clockwise direction, the steepness of the helix being such that each bundle rotates about ¼ of the stem circumference during a distance of about 15 cm. This helical path had been indicated by several earlier workers (e.g., Meneghini, 1836; Nägeli, 1858), but irregularly and only for single bundles. Ciné analysis shows it to be a uniform property of all bundles. It is quite obvious that if the distance between two successive leaf contacts of the same (major) vertical bundle is a little over 30 cm. this twisting brings the higher contact to the side of the stem opposite that which bears the lower contact (cf. Mirbel's diagram, FIG. 1B). If the path is still longer, the bundle may actually return to the original side of the stem. Monoyer's diagram of the upper part of the stem of *Arecastrum* (FIG. 2, right) may be simply the expression of either longer distances between leaf-trace intervals and/or a steeper helix.

DETAILS OF VASCULAR BUNDLE ANATOMY

FIGURE 5 shows three bundles drawn to scale, a major, a minor, and an intermediate one. It can be seen that the three traces enter the leaf at different angles. Therefore there is no distinct nodal plexus.

During the oblique outward curve, a bundle forks repeatedly (FIGS. 3, left; 6, 10, 11). The protoxylem-containing branch goes into the leaf as the leaf trace, the metaxylem-containing branches become respectively the continuation of the vertical bundle, *satellite bundles*, and *bridge bundles*. These four types of branches are discussed in the following paragraphs.

Leaf trace. This originates by gradual transformation of the vertical bundle in the following way. Following any vertical bundle upward in the stem, at a point about 10 cm. below the next leaf contact, the first evidence of protoxylem is reached (position 3 in FIG. 3). From this point upward the amount of protoxylem increases continuously. The bundle then reaches its maximum size (position 4, FIG. 3), turns sharply toward the stem periphery and breaks up into several branches. The whole of the metaxylem, but normally none of the protoxylem, passes into these branches. The protoxylem-containing bundle is the direct continuation of the vertical bundle and goes into the leaf as the leaf trace. This means that *there is no continuity of metaxylem between stem and leaf. The leaf is irrigated solely by protoxylem.*[4]

Vertical bundle. Ordinarily, the vertical bundle is the first branch to break off the leaf trace, shortly above the sharp outward turn. It then follows the leaf trace and near the stem periphery abruptly turns upward and continues its course up the stem, repeating the cycle (FIGS. 3–6).

In most cases a single vertical bundle arises from a trace plexus. Oc-

[4] See footnote 3, page 168.

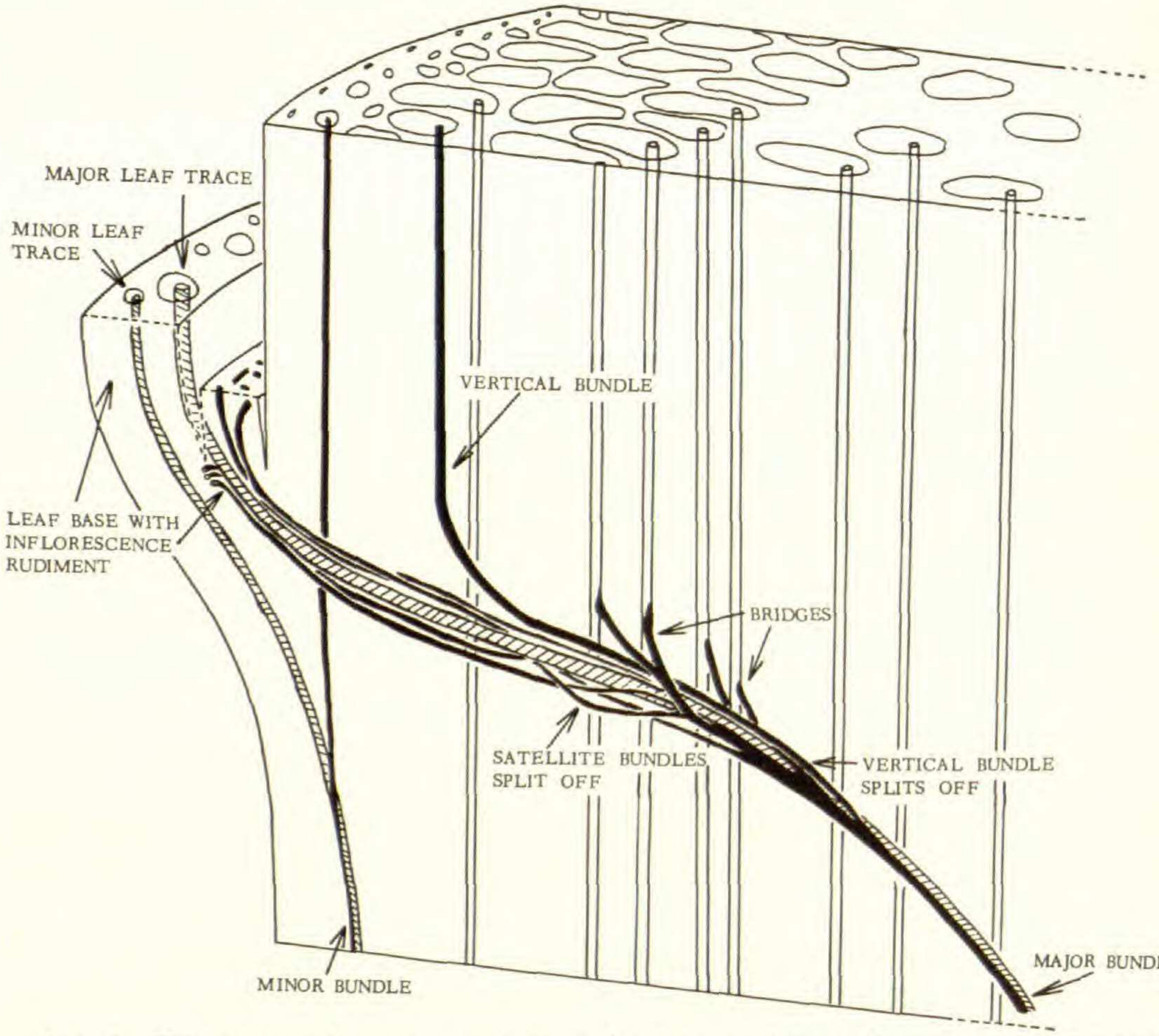


FIG. 6. Diagrammatic representation (not to scale) of the relation of a major leaf trace to its neighboring bundles. Stem axis foreshortened about four times in relation to stem radius. Metaxylem-containing bundles black, protoxylem-containing bundle cross-hatched, neighboring bundles white. The lines indicate direction and continuity of vascular tissue, they do not imply continuous vessels (see text p. 173). This figure represents stages 4–7 of FIG. 3.

casionally, however, none of the branches develops into a vertical bundle, in yet other cases two or even three vertical bundles may arise. This emphasizes the dynamic flexibility of the palm stem: the total number of bundles does not have to be exactly the same along the stem; in fact, it is certainly affected by environmental conditions. Whether the initial drastic increase in stem diameter from seedling to mature axis is due to this mechanism of "multiplying vertical branches" we do not know. Future investigation should answer this question.

Occasionally one can find a vertical bundle carrying not only metaxylem but also protoxylem. This indicates that the distance to its next higher leaf contact is less than 10 cm.

The very small fibrous bundles in the cortical area (FIG. 7) are vertical bundles from minor leaf traces. They become smaller, "move" towards the stem periphery (rather than towards the center) and end blindly further up the stem.

Bridge bundles. From each departing leaf trace, two to six bundles branch off and connect to vertical bundles in the neighborhood (FIG. 6).

Bridges are short, the longest one measured 4.5 mm. Occasionally they are so short that leaf trace and vertical bundle appear to fuse directly (Fig. 10). Bridges are always oriented obliquely upwards in the same way, so that the end of the bridge attached to the leaf trace is below the end attached to the vertical bundle.

Bridge bundles normally come directly off the leaf trace, but they also may break off a satellite bundle or even the vertical bundle. Occasionally a single bridge bundle breaks up into two branches which then connect to two vertical bundles (Fig. 6).

Physiologically, bridge bundles not only provide vertical vascular continuity via other vertical bundles, but they also provide extensive cross connections. Injection experiments in which dyes are introduced via petiole, root, or bore-hole in the stem, illustrate these lateral interconnections quite dramatically. In order to avoid any misunderstanding, we might point out here that by "vascular continuity" we do not mean continuity of individual vessels. Vessels are of limited length and overlap within any one bundle, just as they do within the xylem of a diffuse-porous dicotyledonous tree.

Satellite bundles. Several satellites branch from larger leaf traces in the region of bridge production (Figs. 3, left; 6, 11). Major traces produce up to 10 or more satellites; minor traces produce fewer or none, according to their size. Satellites accompany the trace to the periphery of the central cylinder. Some may "rotate" around the parent leaf trace and, in addition, may be inverted temporarily. They retain their individuality but may become temporarily enclosed within the fibrous sheath of the parent leaf trace or a nearby vertical bundle without making vascular connection. Ultimately they form a "halo" around the leaf trace (Fig. 3, position 6; Fig. 9). Immediately below the leaf base they turn abruptly and tangentially, and enter the inflorescence rudiment. It is obvious that satellites are best developed if a fully developed inflorescence is (or was) present. However, even inflorescences which had aborted very early in their development and are macroscopically not visible can be detected by their satellites, even in the lower "vegetative" part of the aërial stem (Fig. 8).

With a good deal of experience, one can often easily distinguish, in a single transverse section, vertical bundle, satellites, and bridges. However, this is not always possible, and one must follow the bundles upward in order to differentiate with certainty between the three types of branches that come off the leaf trace. One cannot help getting the impression that the three types, vertical bundles, satellites, and bridges, are developmentally equivalent. This problem will undoubtedly be met again, and hopefully be solved, when the apex is analyzed.

COMPARISON OF RHAPIS WITH OTHER MONOCOTYLEDONS

Our study of *Rhapis* has been carried out conjointly with the examination of a number of larger palms. The reason for this is quite obvious.

Our findings differ so fundamentally from the "classical" diagrams (cf. FIGS. 1 and 3) that the question arose as to whether we were dealing with an unusual object. Comparative studies have shown, however, that this is not the case. Whatever we have studied in other species has corresponded to *Rhapis*, although a great deal of work still remains to be done. We are now in a position to do it with the cinematographic method.

Literature search has revealed that the actual observations of former botanists do not differ from our findings. The way in which these early workers put together diagrams by extrapolation and inference proved misleading. Interestingly enough, good observers like Von Mohl, Karsten, etc. describe the limits of their work precisely. Distortions arose by the inaccurate citation of older authors, by frequent re-drawing of diagrams, and by the failure to distinguish what was observed from what was inferred.

Von Mohl's original diagrams (1824) were correct but incomplete. Those showing the blind ending of bundles in a basipetal direction (*Fig. VIII.2* in Tomlinson, 1961, p. 362) can be re-interpreted by assuming that Von Mohl's upper series were of a major bundle (Tomlinson's *Figs. 2a–f*) and the lower series were of a minor bundle (Tomlinson's *Figs. 2g–i*). This is very possible because Von Mohl merely drew a series of bundles from a single section and referred them to a hypothetical scheme. It was only subsequently (Von Mohl, 1849) that he considered the possibility of bundle fusions. This hypothetical suggestion was seized upon by later workers and incorporated in their diagrams (e.g., De Bary, 1877; our FIG. 1E). Branner (1884) is the only nineteenth century worker who fully understood the continuity of vascular bundles, simply because he was able to examine a great deal of material at first hand. He discovered that the continuity of vertical bundles was only evident when the apical regions were examined. Macrodissection suggested the blind ending of bundles because connections are tenuous and easily broken in mature parts of the stem. It is a remarkable feature of botanical history that Branner's very accurate work based on the careful examination of many palms in the field has been entirely overlooked in favor of wholly hypothetical schemes proposed by authors who had little opportunity of examining the problem at first hand.

While one of us (M.H.Z.) is interested in the vascular anatomy of palms from the point of view of long-distance translocation, the other (P.B.T.) approaches the subject as a systematic anatomist. The unravelling of the palm stem via *Rhapis* has given a much sounder theoretical background for an appreciation of certain features tentatively proposed as diagnostically significant (Tomlinson, 1961; cf. also Stenzel, 1904, where the important problem of identifying fossil palm stems is discussed in detail). Palms have been subdivided into three main categories dependent on the presence, in any small sample of the stem, of a majority of vascular bundles with either one, or two, or many vessels. A multi-

dimensional understanding of the palm stem explains this variability. We have seen in *Rhapis* that these three conditions represent successive stages repeated in the same sequence in all bundles over and over again. In *Rhapis* all bundles, traced from below upward and beginning a little above a leaf contact, show initially (FIG. 3, stage 1) one metaxylem vessel, except for areas in which two vessels within one bundle overlap, for example in bridge contacts. Continuing upward, however, the bundle then shows two vessels separated by a parenchymatous isthmus (somewhat below stage 4, FIG. 3). Finally (stages 4 and 5), prior and during the breaking up of the leaf-trace plexus, many metaxylem vessels are present. This increase in the number of vessels upward along a single bundle goes parallel with the increase in the amount of protoxylem.

Diagnostic significance can only be attached to a comparison of bundles of the same stage (preferably stage 1) of two species. Thus *Rhapis*, as well as *Ancistrophyllum*, *Areca*, *Borassus*, etc. (Tomlinson, 1961, p. 336) can be referred to as "one-vessel palms." "Two-vessel palms" can be recognized by protoxylem-free bundles which contain two vessels separated by a parenchymatous isthmus which indicates that the vessels are not merely overlapping ends. There may even be "many-vessel palms," but with the present state of our knowledge comment is not justified.

One great danger of using this difference in number of vessels per vascular bundle (of the stage 1) as a diagnostic feature lies in being satisfied that a small region of the stem is an adequate sample of the whole. In palms, there are considerable quantitative changes from base to apex of a single axis. It is quite conceivable that the same stem could be a "one-vessel" type basally, yet "two-vessel" distally.

The genus *Rhapis* cannot yet be compared easily with monocotyledons like *Zea* (e.g., Kumazawa, 1961) or *Tradescantia* (Scott and Priestley, 1925) which have a plexus of vascular tissue at each node. Non-nodal monocotyledons, however, may be similar, although few of these have been described in sufficient detail to merit comparison. An exception is *Alstroemeria aurantiaca* (Amaryllidaceae) analyzed by Priestley, Scott and Gillett (1935). This shows some of the basic features of the *Rhapis* type. Median leaf traces in *Alstroemeria* are derived from continuous vertical bundles, although this is not obvious because forking occurs many internodes below the node of exsertion. Forking of bundles many nodes below the level of their exsertion as leaf traces is illustrated in Falkenberg's diagrams of several monocotyledons intended as representative of the "palm type." But we know that the one palm (*Chamaedorea*) which Falkenberg claimed to have studied was analyzed incorrectly. We feel justified in being a little suspicious of Falkenberg's diagrams. *Rhapis* still has to be analyzed in terms of developmental physiology in the manner of Priestley and his associates. No doubt in the future many other monocotyledonous shoots will be better understood with the *Rhapis* stem as a model.

SUMMARY

The vascular anatomy of the mature, vegetative aërial axis of *Rhapis excelsa* (Thunb.) Henry is analyzed quantitatively by a cinematographic method. This involves photographing, frame by frame, either sequentially cut surfaces or serial sections stained and mounted permanently. The resulting film is analyzed in a data analyzer. All vascular bundles have essentially the same course and construction. In the uncrowded inner part of the stem they describe a uniform shallow helix continuously through the stem as vertical bundles, tending always toward the center of the stem. At intervals each turns sharply toward a leaf insertion and at the same time breaks up into several branches. The leaf trace proceeds into the leaf, satellite bundles go into the inflorescence, bridge bundles make vascular connection with neighboring bundles, and the vertical bundle continues its way up in the stem, repeating the whole cycle. There are minor, intermediate, and major bundles, the last reach farthest into the stem center and have the longest distances between successive leaf contacts.

ACKNOWLEDGMENTS

Routine serial sectioning on which this analysis is based was carried out by Lesley Jackson, Vroni Oswald, and Gabriel A. Vargo. We are indebted to them for their patience and perseverance with this tedious task.

The generosity of Mrs. A. R. Jennings, who permitted unlimited access to the Coconut Grove Palmetum for supplementary experiments, is gratefully appreciated.

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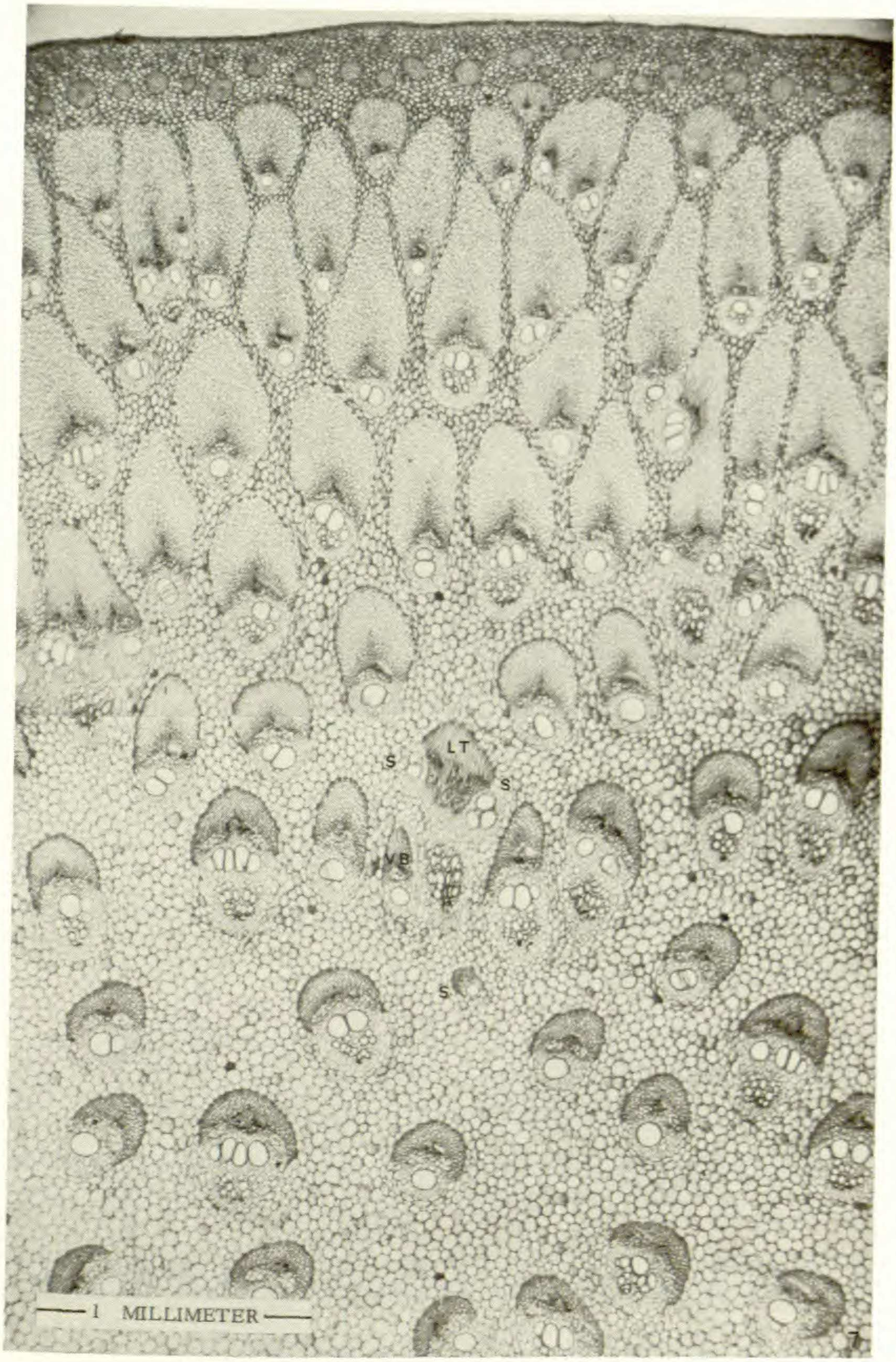
EXPLANATION OF PLATES

PLATE I

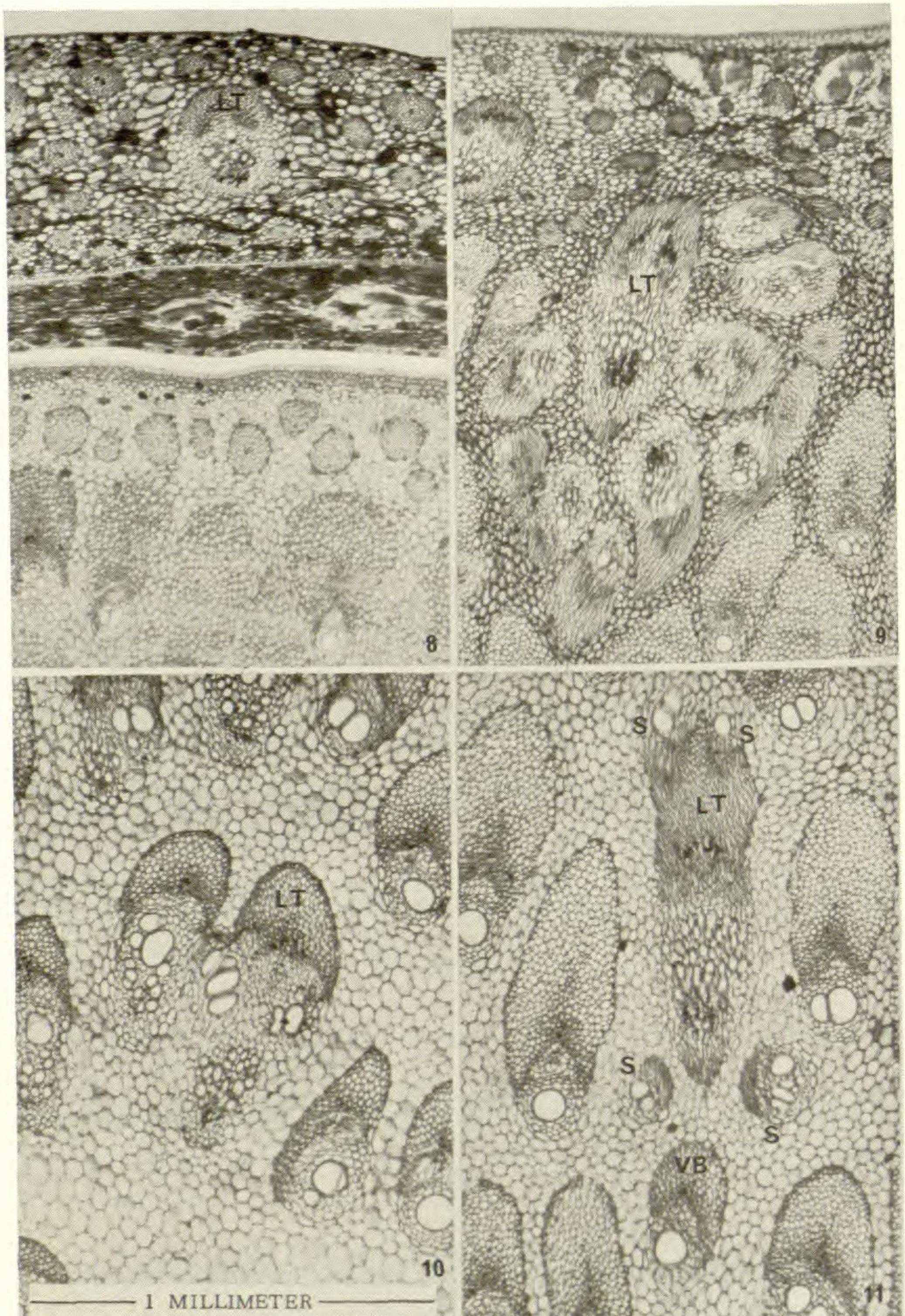
FIG. 7. A small section of the *Rhapis* stem showing crowding of bundles near the stem periphery. Near the center of the photograph a leaf-trace plexus consisting of leaf trace (LT), vertical bundle (VB), and satellite bundles (S). This corresponds to position 5, FIG. 3.

PLATE II

FIGS. 8–11. Transverse sections of stem of *Rhapis*; all magnifications identical. FIG. 8 (top left). A section at the level of the leaf base, corresponding to position 7, FIG. 3. The aborted inflorescence between stem and leaf. FIG. 9 (top right). A section just below the leaf base, corresponding to position 6, FIG. 3. The leaf trace (LT) is surrounded by a halo of satellite bundles. FIG. 10 (bottom left). A short bridge between a leaf trace (LT) and a neighboring vertical bundle. FIG. 11 (bottom right). A leaf-trace plexus consisting of leaf trace (LT), vertical bundle (VB) and satellite bundles (S). This photograph corresponds to position 5, FIG. 3.



ZIMMERMANN & TOMLINSON, THE PALM RHAPIS



ZIMMERMANN & TOMLINSON, THE PALM RHAPIS

STUDIES IN ALYSSUM: NEAR EASTERN REPRESENTATIVES AND THEIR ALLIES, II. SECTION MENIOCUS AND SECTION PSILONEMA

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A SYSTEMATIC SURVEY OF the genus *Alyssum* has long been needed, not only because it is the largest cruciferous genus in Turkey, accounting for approximately one fifth of the taxa of the Cruciferae in that area, but also because it has been the subject of some revisionary work (at least in the perennial species of sections ALYSSUM and ODONTARRHENA). The very extensive, and mostly unidentified Near Eastern collections of P. H. Davis, A. Huber-Morath, and K. H. Rechinger have added impetus to the need for a reassessment of morphological characters and variation, and a more stable definition of the specific and infraspecific taxa.

Previously, the only practical procedure for identifying *Alyssum* was to compare and contrast individual specimens with "correctly determined" herbarium material. The lack of conformity in treatments because of differing interpretations and divergent emphasis placed upon morphological characters is pointedly exemplified by the elaborate taxonomic hierarchies and extreme "splitting" of Fenzl in Tchihatcheff (1860), J. Baumgartner (1907–1911), and E. J. Nyárády (1926–1949). Taxa such as *Alyssum linifolium*, *A. alyssoides*, *A. minus*, *A. minutum*, *A. montanum*, *A. sibiricum*, *A. tortuosum*, *A. murale*, etc., having very wide geographical distributions are subject to considerable morphological variation within and between populations, as well as between individuals.

With the exception of section TETRADENIA, whose component species are not known to occur in Turkey, and section PSILONEMA which is represented in Turkey only by the widespread *Alyssum dasycarpum* (also possibly *A. alyssoides*, cf. page 199), more species (eighty-eight) and endemic species (forty-nine) are found in Turkey than in any other land area of comparable size. Of the seven species assigned to section MENIOCUS, six occur in Turkey, and of these three are endemics. These endemics (*A. blepharocarpum*, *A. stylare* and *A. huetii*) are characterized by a unique fruit indumentum of setae, found only in section MENIOCUS. The other species of this section having the same type of fruit indumentum is *A. heterotrichum* from Iran, Afghanistan, and a part of Kazakh S. S. R. The remaining three species of section MENIOCUS are glabrous-fruited. Of these, *A. aureum* and *A. meniocoides* have continuous distributions from southern Turkey to Syria, Lebanon, Palestine, Iraq, and Iran, while *A. linifolium* is one of the most widespread in the genus, extending from England (where it was probably introduced) throughout Europe and Asia, and east to India. It is probable that as Turkey has the largest

representation of species and endemics of section MENIOCUS, it has been the center of speciation for that section. Certainly, Turkey is the current center of diversity. On the other hand, this is not true for section PSILONEMA, of which only one species is known definitely to occur in Turkey. Whereas *Alyssum granatense* is found only in Spain and North Africa, *A. damascenum* and *A. homalocarpum,* although both Oriental species, are to be considered as Saharo-Sindian elements, and are not known from Turkey.

The widespread taxa *Alyssum linifolium* of section MENIOCUS, and *A. alyssoides* and *A. dasycarpum* of section PSILONEMA are characterized by a wide range of environmental tolerance. Such species as *A. aureum* and *A. meniocoides* which have more or less continuous distributions from Turkey into adjacent regions and are steppe-inhabiting or Irano-Turanian elements, are relatively limited by particular habitat preferences. This is also true for the Turkish endemics of section MENIOCUS, which although found in spatially open habitats, are characterized by a narrow range of environmental tolerance. All species of sections MENIOCUS and PSILONEMA are essentially calcicolous. This feature is particularly pronounced in Turkey where the species of section MENIOCUS are usually found on calcareous substrates, and is correlated with their preference for the steppe, the soils of which are primarily of limestone structure. The very widespread *A. linifolium* and *A. dasycarpum* attain their maximum development in the calcareous steppe and serpentine mountain screes, but tolerate and are relatively abundant in the saline steppe. Similarly, *A. blepharocarpum* is known to occur in the salt impregnated portions of the steppe which surrounds many lakes of the Turkish interior.

In this and succeeding papers, the strictly European or Asiatic species, which are most closely allied to those occurring in Turkey are included in the keys, and are treated systematically. However, these studies of *Alyssum* must be regarded primarily as a systematic revision of the Turkish species.

To assist in interpretation of the keys and descriptions, in this paper and in those to come, three plates showing the morphological diversity of petals, filaments, fruits, and trichomes are included. These plates illustrate only the major types of diversity of these structures throughout the genus. PLATES II and III show some of the diversity of the distinguishing floral and fruit characters. PLATE IV illustrates basic hair types which comprise the indumentum. These types are arranged more or less in a progressional sequence, from the simplest to the most complex. This does not imply, however, that one type necessarily evolved directly from any other. Many of the fruits pictured in PLATE III are normally covered with a characteristic indumentum (FIGS. a, c–g, j-o). This indumentum has been omitted in order that the fruit shape and configuration not be obscured. I am grateful to Dr. P. H. Davis, University Department of Botany, Edinburgh, Scotland, for permitting the use of these three plates, which were drawn for the forthcoming *Flora of Turkey* by Mrs. A. Dyer.